



# Biological control of sentinel egg masses of the exotic invasive stink bug *Halyomorpha halys* (Stål) in Mid-Atlantic USA ornamental landscapes



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## HIGHLIGHTS

- Sentinel egg masses were placed in plots comprised of native or exotic plants.
- Parasitism and predation rates were not affected by plot type or plant genus.
- Parasitism rates were higher in adjacent wooded sites than in experimental plots.
- Seven native and one exotic parasitoid species attacked sentinel egg masses.
- Parasitism and predation rates in experimental plots and wooded sites were low.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Biological invasions have far reaching effects on native plant and arthropod communities. This study evaluated the effect of natural enemies on eggs of the exotic invasive brown marmorated stink bug *Halyomorpha halys* (Stål) in experimental plots comprising species pairs of 16 ornamental trees and shrub genera from either Eurasia or North America and in wooded areas adjacent to the plots. Sentinel egg masses were placed on leaves of *Acer*, *Cercis*, *Hydrangea*, and *Prunus* in the plots and in seven genera of trees and shrubs in adjacent woods. Overall, rates of parasitism and predation in experimental plots were low, accounting for only 3.8% and 4.4% of egg mortality, respectively. There were no significant differences in parasitism and predation rates between native or exotic plots or between plants of different genera. In 2015, predation was significantly higher in the experimental plots than in the wooded sites, but parasitism was significantly higher in the wooded sites. In the experimental plots, seven native and one exotic parasitoid species attacked sentinel egg masses. Six native parasitoid species attacked sentinel egg masses in the wooded sites. Parasitoids in the genus *Trissolcus* were more likely to attack egg masses in exotic plots than in native plots. There is no evidence that native natural enemies attacking eggs of the exotic BMSB were more prevalent in landscapes with native ornamental trees and shrubs than those with exotic trees and shrubs.

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## 1. Introduction

Urban landscapes often comprise mosaics of exotic and native plants. There is evidence that exotic plants reduce the abundance and species diversity of arthropod communities (Zeufele et al., 2008; Burghardt et al., 2010; Simao et al., 2010; Roberge and Stenbacka, 2014; Macedo-Veiga et al., 2016). However, the effects of exotic plants on the abundance and species diversity of native parasitoids and predators of herbivorous insects are largely unknown (Bezemer et al., 2014). In a two-year study comparing the attractiveness of native and exotic plants to natural enemies, many of the native perennials were more attractive to natural enemies than annual exotic plants due to their nectar and pollen resources (Fiedler and Landis, 2007a). Natural enemy abundance increased with increasing floral area, period of peak bloom, maximum flower height, and decreasing corolla width (Fiedler and Landis, 2007b). Simao et al. (2010) conducted a study in 32 5.25 m × 5.25 m mowed plots that were planted with seeds from 12 native herbaceous plants. In half of these plots, seeds of the invasive exotic Japanese stiltgrass *Microstegium vimineum* (Trin) A. Camus were also planted. In plots with the invasive grass, insect populations were significantly lower than in plots composed exclusively of native plants. However, the impact of the invasive grass was greater on natural enemy populations, resulting in a reduction of 61%, compared with a reduction of only 31% in populations of herbivorous insects (Simao et al., 2010). In contrast, Lescano and Farji-Brener (2011) determined that the abundance of ants was increased on exotic thistles compared with native plants due to higher population densities of aphids on these invasive plants.

The ability of natural enemies to find their native prey or hosts on exotic plants can be reduced if they fail to recognize visual and chemical cues emitted by the plant that provide information about the presence of their prey or hosts (Vet and Dicke, 1992). Spatial features of the landscape can also interfere with the searching behavior of natural enemies. In patches of habitat where native grass was surrounded by invasive grass, both the native herbivore and its parasitoid suffered high rates of extinction, but the rate of extinction of the parasitoid was three times higher than that of its host (Cronin and Haynes, 2004). The native butterfly *Pieris oleracea* Harris (Lepidoptera: Pieridae) was able to find refuge from parasitism on an exotic plant because overtopping vegetation prevented the parasitoid from finding its host (Herlihy et al., 2014).

The development and survival of parasitoids depends on the fitness of the host feeding on the plant. For example, the survival of the larval parasitoid *Cotesia glomerata* L. (Hymenoptera: Braconidae) and its host *Pieris brassicae* (L.) were much lower when *P. brassicae* was reared on an exotic plant than a native plant (Fortuna et al., 2012). Also, the parasitism rate of *C. glomerata* on *P. brassicae* larvae was higher on the native plant than on the exotic plant in field cage tests (Fortuna et al., 2013). In contrast, the survival of the pupal parasitoid *Pteromalus puparum* L. (Hymenoptera: Pteromalidae) was similar on *P. brassicae* reared on exotic and native plants (Fortuna et al., 2012).

We tested the hypothesis that native natural enemies would be more abundant in urban landscapes composed of native plants than in those composed of exotic plants by placing sentinel egg masses of the exotic invasive brown marmorated stink bug (BMSB) *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) on plants in experimental plots composed exclusively of either native or exotic ornamental trees and shrubs. This study is one part of a replicated experiment testing the hypothesis that native natural enemies will be more abundant and diverse in habitats comprising native than exotic woody ornamental landscape plants (MHG, unpublished).

BMSB was first discovered in the United States in 1996 in Allentown, PA (Hoebeke and Carter, 2003). It is an extremely

polyphagous pest of agricultural crops and ornamental plants (Hoebeke and Carter, 2003; Leskey et al., 2012a, 2012b; Rice et al., 2014; Wallner et al., 2014; Xu et al., 2014). Adults have been found feeding on over 100 ornamental trees and shrubs (Bergmann et al., 2016a). A survey of ornamental trees and shrubs identified 88 species used by all life stages of BMSB, including species of *Acer* and *Cercis* (Bergmann et al., 2016b). A survey of trees and shrubs in a commercial nursery found that species of lilac and maple (*Syringa*, *Acer*; Sapindales: Sapindaceae), redbud (*Cercis*; Fabales: Fabaceae), London plane tree (*Platanus*; Proteales: Platanaceae), and ornamental cherry (*Prunus*; Rosales: Rosaceae) were most commonly used by BMSB adults (USDA APHIS PPQ, 2010).

Sentinel BMSB egg masses were placed on plants from three genera, *Acer*, *Cercis*, *Prunus*, that were most frequently used by BMSB (USDA APHIS PPQ, 2010). In addition, sentinel egg masses were placed on *Hydrangea*, a very common plant in yards and gardens. The effect of natural enemies on BMSB eggs in native and exotic plots was evaluated by comparing the proportion of eggs attacked by parasitoids and predators for each plant genus in both native and exotic plots. We also compared the rates of parasitism and predation on egg masses in the experimental plots with egg masses placed in adjacent wooded areas.

We evaluated the species composition of native parasitoids attacking BMSB eggs in exotic and native plots and in wooded areas adjacent to the experimental plots to determine if habitat influenced the parasitoid species complex. Previous studies have found that *Telenomus podisi* Ashmead (Hymenoptera: Scelionidae) is the predominant parasitoid in vegetable crops and *Trissolcus* spp. are dominant in wooded habitats bordering those crops (Talamas et al., 2015; Herlihy et al., 2016). In a study conducted in ornamental tree nurseries in Maryland, *Anastatus* spp. (Hymenoptera: Eupelmidae) were the predominant parasitoids attacking BMSB egg masses (Jones et al., 2014). In Georgia, *Anastatus* spp. attacked native stink bug eggs in woodland habitats, but not in crops, and *T. podisi* was the predominant parasitoid species in both crops and woodland habitats (Tillman, 2016).

In addition, we collected parasitoids that were attending BMSB egg masses. Studies have shown that scelionid parasitoids of pentatomids defend egg masses they have attacked from other parasitoids (Austin et al., 2005). For instance, the parasitoid *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) frequently remains on the egg mass after oviposition, patrols the egg mass, and aggressively defends the egg mass against intruders (Field, 1998; Field et al., 1998).

## 2. Materials and methods

### 2.1. Locality

We performed the experiment at the United States National Arboretum (USNA) in Northeast Washington, D.C., USA (38° 54' 36.84" N 76° 58' 3.14" W) in U.S.D.A. plant hardiness zone 7a (avg. annual minimum temperature of −17.8 to −15 °C). The USNA is uniquely suited for urban study: it is located within a large city, is itself a model urban landscape, and contains hundreds of examples of exotic and native congeners of popular urban landscape plants, including many of those in our experiment. Hence many herbivores and natural enemies capable of colonizing the experiment are found in the surrounding landscape, as they are in real-world urban residential plots.

### 2.2. Plants

Plots were planted with woody species commonly used as ornamental trees and shrubs in urban landscapes. We included only

**Table 1**  
Plant species in the experimental plots.

Stratum	Native	Exotic
<b>Overstory Trees</b>	<i>Acer saccharum</i> Marshall	<i>Acer platanoides</i> L.
	<i>Quercus alba</i> L.	<i>Quercus robur</i> L.
	<i>Catalpa bignonioides</i> Walter	<i>Catalpa ovata</i> G. Don
	<i>Prunus virginiana</i> L.	<i>Prunus padus</i> L.
	<i>Ilex opaca</i> Aiton	<i>Ilex aquifolium</i> L.
	<i>Liriodendron tulipifera</i> L.	<i>Liriodendron chinense</i> (Hemsl.) Sarg.
	<i>Pinus strobus</i> L.	<i>Pinus wallichiana</i> A.B. Jacks.
	<i>Picea glauca</i> (Moench) Voss.	<i>Picea abies</i> L.
<b>Understory Trees</b>	<i>Cercis canadensis</i> L.	<i>Cercis chinensis</i> Bunge
	<i>Cornus florida</i> L.	<i>Cornus kousa</i> Hance
<b>Woody Shrubs</b>	<i>Hydrangea arborescens</i> L.	<i>Hydrangea paniculata</i> Siebold
	<i>Juniperus virginiana</i> L.	<i>Juniperus chinensis</i> L.
	<i>Callicarpa americana</i> L.	<i>Callicarpa japonica</i> Thunb.
	<i>Viburnum dentatum</i> L.	<i>Viburnum dilitatum</i> Thunb.
<b>Woody Vines</b>	<i>Campsis radicans</i> (L.) Seem ex Bureau	<i>Campsis grandiflora</i> (Thunb.) K. Schum.
	<i>Wisteria frutescens</i> (L.) Poir.	<i>Wisteria floribunda</i> (Willd.) DC
<b>Turf Grass</b>	<i>Festuca arundinacea</i> Schreb.	<i>Festuca arundinacea</i> Schreb.

species that are available in the nursery trade, so that the results of this research would be relevant to planting and management choices in urban landscapes (Table 1). We planted matched species pairs from 16 genera that had been geographically separated for at least a million years and are as phylogenetically-related as possible. The only exception to this one-to-one congeneric match is the turf, because no native turf grasses are adapted to the relatively

high summer temperatures and humidity of the study area. In order to increase the plant-based resources available to natural enemies, we included four genera with extrafloral nectaries: *Campsis*, *Prunus*, *Liriodendron*, and *Catalpa*.

### 2.3. Design of experimental plots

The experiment was set up in a randomized complete block design, with one replicate of each treatment in each of three blocks (Azalea, Valley, Conifer) to control for location effects due to differences in soil, slope, exposure, and surrounding vegetation mosaic. The shortest distance between blocks ranged from 300 to 900 m. The plots measure 25 m × 25 m, which is equivalent to the vegetated area of a 0.2 acre (0.08 ha) single-family residential lot in the Chesapeake Bay watershed (Cappiella and Brown, 2001). Plots were planted with the selected trees, shrubs, and turf, arrayed on the plot to simulate an urban backyard, with overstory trees around the edges and in the corners, an arbor in the center for climbing vines, and mulched central and peripheral beds for understory trees and shrubs. Each plot was surrounded by a ten-meter-wide buffer of mowed meadow on the back and sides and bounded in front by a hard-surfaced road to simulate the impact of impervious surfaces on arthropod migration and any other, unknown aspects of urban ecosystem function. In order to meet requirements of the USNA, which is an exhibit space as well as a research facility, a 2.0 m buffer of closely mowed meadow separates the front of each plot from the road. Within each block, the plots were separated by a minimum of 50 m (maximum 99 m) of lightly managed meadow, which we consider close enough to ensure that they inhabit the same experimental block, while providing separation between them by an extent of unfavorable habitat that is larger than that found between most residential lots in the region (Fig. 1).



**Fig. 1.** A pair of native and exotic 25 m × 25 m experimental plots from the Valley block; All plots are bounded in front with hard-surfaced road and on the sides and back by 10-m wide mowed meadow buffers as shown in this example.





**Fig. 2.** The USDA indicating the wooded sites for the three blocks (Azalea, Conifer, Valley) with yellow pins. Each wooded site was adjacent to a pair of experimental plots.

#### 2.4. Wooded sites

Wooded sites were within 2–10 m of the edge of second-growth woods, and a mean of  $83 \pm 25.0$  m distant from adjacent experimental plots (Fig. 2). The Azalea block was mesic woods, the Valley block was hydric (floodplain) woods, and the Conifer block was a xeric hillside woods; the plant species used for egg sentinel placement are noted below.

#### 2.5. Sentinel egg masses

Fresh BMSB egg masses (<24 h of age) of BMSB were obtained from a laboratory colony maintained at the Beltsville Agricultural Research Center (BARC), Beltsville, MD. Females oviposited on either paper towel or filter paper placed in 6-liter cylindrical clear polystyrene containers (Pioneer Plastics, Dixon, KY). BMSB were reared in an incubator (16: 8 h [L:D]; 25 °C) and supplied with green beans, water vials plugged with cotton, and seed paper (hulled sunflower seeds and buckwheat seeds attached to brown packaging paper (Kraft paper, Staples, Framingham, MA) with wall paper paste (Golden Harvest, BigPaintStore, Little Chute, WI). Every two weeks, three freshly laid egg masses were obtained from the colony and kept in an incubator (16: 8 h [L:D]; 26 °C) to calculate egg viability. Using a dissecting microscope, the number of intact eggs in each egg mass was recorded, excluding eggs that were collapsed or damaged in the laboratory prior to field placement.

#### 2.6. Sentinel egg mass placement and evaluation

In experimental plots, sentinel egg masses were placed in the field for 72 h every other week from the first week of June in 2014 and 2015 through the first week of September in 2014 and the last week of August in 2015. On each sampling date, 24 freshly laid egg masses were placed on one of eight plant species on each

of the three blocks, with each block comprising one native and one exotic plot. Sentinel egg masses were placed on species pairs from four plant genera: *Acer saccharum* Marshall (native) and *Acer platanoides* L. (exotic) (Sapindales: Sapindaceae); *Cercis canadensis* L. (native) and *Cercis chinensis* Bunge (exotic) (Fabales: Fabaceae); *Hydrangea arborescens* L. (native) and *Hydrangea paniculata* Siebold (exotic) (Cornales: Hydrangeaceae); *Prunus virginiana* L. (native) and *Prunus padus* L. (exotic) (Rosales: Rosaceae) (Table 1). During the week of 12 August 2014, a decline in production resulted in seven missing egg masses. We assigned the missing plants by means of a table of random numbers, such that no plant species was missed more than once across the three blocks.

In wooded sites adjacent to each pair of experimental plots, six egg masses, two on each of the three most abundant woody species recorded as hosts of BMSB, were placed in the field every other week (synchronous with landscape plots) from the first week of June to the second week of September in 2015 only, except for the week of 23 July, for which only three egg masses per site were placed out, due to a shortage of egg masses. Species used (all but one North American native species) were red maple (*Acer rubrum* L.; Azalea and Valley blocks), black cherry (*Prunus serotina* Ehrhart; Azalea and Conifer sites), serviceberry (*Amelanchier canadensis* (L.) Medik; Rosales: Rosaceae; Azalea block), buckeye (*Aesculus flava* Aiton; Sapindales: Sapindaceae) and bush honeysuckle (non-native *Lonicera maackii* (Rupr.) Herder; Dipsacales: Caprifoliaceae; Valley site), American holly (*Ilex opaca* Aiton; Aquifoliales: Aquifoliaceae) and tupelo (*Nyssa sylvatica* Marshall; Cornales: Cornaceae; Conifer block).

Egg masses were attached with two 4.8 cm-long wooden clothespins (Darice, Inc., Strongsville, Ohio) in landscaped plots, and pinned using a sewing pin (adjacent woods) to the abaxial surfaces of one leaf on one individual of each of the eight plant species in all three blocks, between 1.2 m and 1.8 m above the ground on the trees, and in the upper third of the canopy on *Hydrangea*.

Each egg mass was visited mid-morning and mid-afternoon on each of the following two days, and again on the third morning, at which time any parasitoids found attending egg masses were collected and preserved in 80% ethanol for later species identification. These parasitoids were possibly guarding egg masses against other parasitoids.

Egg masses were collected from the field after 72 h. Egg masses collected in plots were placed in Petri dishes and those collected in wooded areas were placed in zipper-topped plastic bags. All egg masses were returned to the laboratory, where they were examined under a microscope and the number of intact eggs and eggs damaged by either chewing predators (broken) or sucking predators (collapsed) were recorded. Egg masses with intact eggs were kept in an incubator (16: 8 [L:D] h; 26 °C) to record nymphal and parasitoid emergence. When parasitoids emerged, they were placed in vials with 95% ethanol for later species identification. Any egg masses with intact eggs that might have contained either undeveloped or fully developed parasitoids that failed to emerge successfully were dissected. Dead nymphs and partially and fully developed parasitoids were recorded. When possible, parasitoids found by dissection were identified. However, parasitism may have occurred without any visible evidence of parasitoid development in some cases.

## 2.7. Statistical analysis

The effect of natural enemies on BMSB eggs for both experimental plots and wooded sites was calculated based on the total number of eggs per mass with nymphal emergence, parasitism or predation. Nymphal emergence, predation, and parasitism were used as dependent variables in a generalized linear mixed effects ANOVA model with block (Azalea, Valley, and Conifer) as a random block effect and sampling dates as repeated measures using a negative binomial distribution, log link function, and log total eggs offset. When a predominant number of zero counts was observed, the value 0.1 was added to all counts (both the dependent variable and the offset) to avoid incorrectly large variability estimates produced by the log link function in regions near zero.

The habitat preferences of parasitoid species were determined based on the total number of egg masses parasitized by each

species. The species composition of parasitoids in landscaped and wooded sites and in exotic and native plots was compared using a generalized linear model with binary distribution and logit link. The rate of emergence of the four predominant parasitoid species was determined based on the numbers of parasitoids that were able to successfully emerge from egg masses known to be parasitized by that species based on species identifications from emerged and dissected parasitoids. The numbers of parasitoids of the four species emerging per egg mass were compared using a generalized linear model with negative binomial distribution and log link.

All generalized linear models were fit using SAS PROC GLIMMIX (SAS, 2012). Means comparisons of interest were obtained, either via the LSMEANS statement or by specifying the associated contrast, using mean estimates conditioned on the random effects (Stroup, 2013, 2015).

## 3. Results

### 3.1. Experimental plots

Prior to field placement, the mean ( $\pm$  SE) number of eggs per mass was  $26.6 \pm 0.2$ . Of 352 sentinel egg masses placed in landscaped plots, five were lost. Of the 347 egg masses recovered, 42 had at least one egg parasitized and 73 had at least one egg damaged by predators. The nymphal emergence rate from laboratory-reared egg masses was  $79.7 \pm 3.4\%$  compared with  $57.4 \pm 2.1\%$  for sentinel egg masses in 2014–2015. Overall rates of egg mortality attributed to parasitism ( $3.8 \pm 0.8\%$ ) and predation ( $4.4 \pm 0.9\%$ ) were low. The proportion of eggs with emerged parasitoids was  $3.0 \pm 0.7\%$  compared with only  $0.8 \pm 0.2\%$  for dissected parasitoids. Mean ( $\pm$ SE) egg mortality due to unknown causes was  $34.4 \pm 1.9\%$ . However, an average of 20.3% of eggs from the laboratory colony failed to hatch even when egg masses were kept in an incubator under optimal conditions.

Nymphal emergence, predation, and parasitism rates were evaluated by year, month, plot (exotic and native), and plant genus (*Acer*, *Cercis*, *Hydrangea*, and *Prunus*) (Table 2). Overall, there were no significant differences in nymphal emergence, predation, or parasitism rates between exotic and native plots or among plant

**Table 2**

Mean ( $\pm$ SE) percent nymphal emergence, predation, and parasitism of total eggs per egg mass per year (2014, 2015), month (June, July, August) on each plant genus (*Acer*, *Cercis*, *Prunus*, and *Hydrangea*) in native and exotic experimental plots.

Variable	Plot	Plant Genus	June 2014	July 2014	August 2014	June 2015	July 2015	August 2015
Nymphal Emergence	Exotic	<i>Acer</i>	35.8 $\pm$ 22.0	65.6 $\pm$ 13.2	76.1 $\pm$ 10.5	85.9 $\pm$ 3.2	27.5 $\pm$ 13.0	35.6 $\pm$ 14.0
Nymphal Emergence	Exotic	<i>Cercis</i>	40.2 $\pm$ 18.9	53.8 $\pm$ 11.6	88.8 $\pm$ 5.9	67.1 $\pm$ 12.3	48.8 $\pm$ 17.4	30.5 $\pm$ 14.2
Nymphal Emergence	Exotic	<i>Hydrangea</i>	35.1 $\pm$ 20.0	44.3 $\pm$ 13.8	70.8 $\pm$ 12.7	68.9 $\pm$ 11.3	54.6 $\pm$ 16.3	38.2 $\pm$ 13.5
Nymphal Emergence	Exotic	<i>Prunus</i>	61.6 $\pm$ 18.2	73.0 $\pm$ 8.3	71.0 $\pm$ 15.7	57.1 $\pm$ 14.0	70.9 $\pm$ 14.6	39.3 $\pm$ 14.0
Nymphal Emergence	Native	<i>Acer</i>	53.6 $\pm$ 18.7	60.1 $\pm$ 12.0	55.8 $\pm$ 15.8	63.0 $\pm$ 15.6	50.3 $\pm$ 14.3	37.0 $\pm$ 15.9
Nymphal Emergence	Native	<i>Cercis</i>	56.2 $\pm$ 17.9	54.2 $\pm$ 13.5	79.8 $\pm$ 13.1	87.9 $\pm$ 4.7	46.4 $\pm$ 18.0	13.1 $\pm$ 13.1
Nymphal Emergence	Native	<i>Hydrangea</i>	37.5 $\pm$ 19.5	69.7 $\pm$ 13.4	63.1 $\pm$ 16.7	69.3 $\pm$ 11.5	58.3 $\pm$ 19.0	41.1 $\pm$ 19.0
Nymphal Emergence	Native	<i>Prunus</i>	55.6 $\pm$ 20.5	55.1 $\pm$ 12.7	91.4 $\pm$ 5.5	61.5 $\pm$ 10.9	31.0 $\pm$ 18.7	16.7 $\pm$ 16.7
Parasitism	Exotic	<i>Acer</i>	5.1 $\pm$ 3.2	1.4 $\pm$ 1.4	0.0 $\pm$ 0.0	0.4 $\pm$ 0.4	12.6 $\pm$ 12.6	8.4 $\pm$ 7.6
Parasitism	Exotic	<i>Cercis</i>	18.9 $\pm$ 18.9	0.4 $\pm$ 0.4	0.0 $\pm$ 0.0	1.6 $\pm$ 1.6	6.0 $\pm$ 6.0	0.6 $\pm$ 0.6
Parasitism	Exotic	<i>Hydrangea</i>	0.8 $\pm$ 0.8	3.9 $\pm$ 2.3	11.2 $\pm$ 10.2	0.0 $\pm$ 0.0	1.9 $\pm$ 1.3	0.0 $\pm$ 0.0
Parasitism	Exotic	<i>Prunus</i>	2.2 $\pm$ 2.2	0.7 $\pm$ 0.7	8.7 $\pm$ 8.7	4.4 $\pm$ 2.3	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
Parasitism	Native	<i>Acer</i>	0.0 $\pm$ 0.0	1.2 $\pm$ 1.2	0.0 $\pm$ 0.0	8.6 $\pm$ 8.6	1.0 $\pm$ 1.0	0.0 $\pm$ 0.0
Parasitism	Native	<i>Cercis</i>	0.0 $\pm$ 0.0	3.2 $\pm$ 2.8	10.1 $\pm$ 9.4	0.4 $\pm$ 0.4	11.3 $\pm$ 11.3	0.0 $\pm$ 0.0
Parasitism	Native	<i>Hydrangea</i>	12.7 $\pm$ 12.7	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
Parasitism	Native	<i>Prunus</i>	7.1 $\pm$ 7.1	10.4 $\pm$ 6.9	2.7 $\pm$ 2.7	11.6 $\pm$ 11.6	14.3 $\pm$ 14.3	0.0 $\pm$ 0.0
Predation	Exotic	<i>Acer</i>	0.0 $\pm$ 0.0	0.4 $\pm$ 0.4	0.0 $\pm$ 0.0	0.9 $\pm$ 0.9	0.6 $\pm$ 0.6	6.9 $\pm$ 3.7
Predation	Exotic	<i>Cercis</i>	0.0 $\pm$ 0.0	1.0 $\pm$ 0.7	0.4 $\pm$ 0.4	0.4 $\pm$ 0.4	19.7 $\pm$ 16.1	36.8 $\pm$ 20.1
Predation	Exotic	<i>Hydrangea</i>	0.0 $\pm$ 0.0	10.4 $\pm$ 10.0	0.0 $\pm$ 0.0	1.4 $\pm$ 1.4	6.8 $\pm$ 3.7	6.2 $\pm$ 2.9
Predation	Exotic	<i>Prunus</i>	0.0 $\pm$ 0.0	1.5 $\pm$ 1.0	0.0 $\pm$ 0.0	1.6 $\pm$ 0.9	0.6 $\pm$ 0.6	6.2 $\pm$ 2.9
Predation	Native	<i>Acer</i>	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.5 $\pm$ 0.5	0.0 $\pm$ 0.0	9.9 $\pm$ 8.1	2.5 $\pm$ 2.5
Predation	Native	<i>Cercis</i>	0.0 $\pm$ 0.0	0.8 $\pm$ 0.5	5.9 $\pm$ 3.9	0.4 $\pm$ 0.4	6.0 $\pm$ 5.3	33.9 $\pm$ 20.9
Predation	Native	<i>Hydrangea</i>	0.0 $\pm$ 0.0	1.0 $\pm$ 0.7	0.5 $\pm$ 0.5	3.0 $\pm$ 2.3	2.4 $\pm$ 1.8	11.3 $\pm$ 10.6
Predation	Native	<i>Prunus</i>	16.7 $\pm$ 16.7	1.6 $\pm$ 1.0	3.6 $\pm$ 3.1	3.2 $\pm$ 1.7	17.3 $\pm$ 16.6	16.7 $\pm$ 16.7

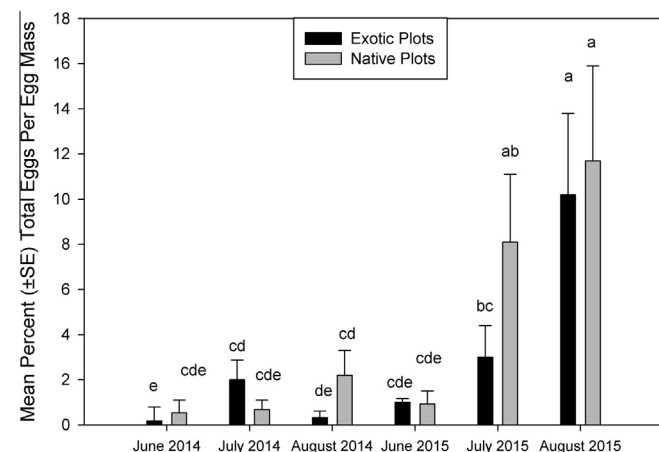
**Table 3**  
F statistics and P values from a generalized linear mixed effects ANOVA model testing the effects of year (2014, 2015), month (June, July, August), block (Azalea, Conifer, Valley), plant genus (*Acer*, *Cercis*, *Prunus*, and *Hydrangea*) and plot (native or exotic) on nymphal emergence, parasitism and predation rates from sentinel egg masses.

Source	DF	F Statistic			P value <sup>a</sup>		
		Nymph	Parasitism	Predation	Nymph	Parasitism	Predation
Plot	1, 95	0.85	0.41	2.11	0.36	0.52	0.15
Plant Genus	3, 95	0.12	0.79	2.25	0.95	0.50	0.09
Year	1, 95	4.88	0.00	22.96	0.03 <sup>*</sup>	0.99	<0.0001 <sup>*</sup>
Month	2, 95	1.55	0.07	6.94	0.21	0.94	0.002 <sup>*</sup>
Year × Plot	1, 95	0.65	0.03	0.25	0.42	0.86	0.62
Year × Plant Genus	3, 95	1.39	2.84	0.56	0.25	0.04 <sup>*</sup>	0.64
Plot × Plant Genus	3, 95	1.13	4.19	2.62	0.34	0.008 <sup>*</sup>	0.05
Year × Plot × Plant Genus	3, 95	1.66	0.38	0.25	0.18	0.77	0.86
Year × Month	2, 95	13.09	1.22	1.6	<0.0001 <sup>*</sup>	0.30	0.21
Plot × Month	2, 95	1.34	0.77	1.1	0.27	0.46	0.34
Year × Plot × Month	2, 95	0.23	0.92	3.98	0.79	0.40	0.02 <sup>*</sup>
Plant Genus × Month	6, 95	0.29	1.34	1.28	0.94	0.25	0.27
Year × Plant Genus × Month	6, 95	0.98	1.77	0.71	0.44	0.11	0.64
Plot × Plant Genus × Month	6, 95	0.71	2.35	0.59	0.64	0.04 <sup>*</sup>	0.74
Year × Plot × Plant Genus × Month	6, 95	1.36	1.49	0.96	0.24	0.19	0.46

<sup>a</sup> Indicates  $P < 0.05$ ; GLIMMIX Procedure.

genera (Table 3). In a comparison of the two years, there were significant differences in nymphal emergence (2014:  $61.7 \pm 2.9\%$ ; 2015:  $52.6 \pm 3.1\%$ ) and predation (2014:  $1.9 \pm 0.8\%$ ; 2015:  $7.2 \pm 1.6\%$ ), but not parasitism (2014:  $3.9 \pm 1.1\%$ ; 2015:  $3.4 \pm 1.1\%$ ) (Table 3). Predation was more than three times higher in 2015 than in 2014.

Seasonal effects on nymphal emergence, predation, and parasitism rates were evaluated for the months of June, July, and August in 2014 and 2015. Twenty-four sentinel egg masses placed in experimental plots on a single date in the first week of September of 2014 were included in the month of August. There were no significant differences in the monthly rates of nymphal emergence or parasitism. However, there was a significant difference in predation rates per month. Predation was significantly higher in August than in June. There was a highly significant interaction between year and month for nymphal emergence rates ( $P < 0.0001$ ), but not for predation or parasitism (Table 3). Nymphal emergence was highest in August 2014 ( $75.0 \pm 4.4\%$ ) and lowest in August 2015 ( $31.4 \pm 5.2\%$ ). There was also a significant interaction between plot, year, and month for predation rates. Predation rates were highest in both native and exotic plots in August of 2015 and lowest in exotic plots in June of 2014 (Fig. 3).



**Fig. 3.** Mean ( $\pm$ SE) percent of total number of eggs per egg mass damaged or removed by predators in exotic and native plots each month over the two-year study; estimated by a generalized linear mixed effects model with negative binomial distribution, log link, and log total eggs offset. Bars with different letters were significantly different (SAS PROC GLIMMIX:  $P < 0.05$ ).

The total number of egg masses known to be parasitized by each species was determined based on identifications of emerged and dissected parasitoids. Only those egg masses recovered (not missing from predation or other causes) were counted as being subject to parasitoid attack. Species composition of parasitoids identified from emerged and dissected parasitoids included four native and one exotic species of *Trissolcus* (Hymenoptera: Scelionidae) (native: *T. brochymenae* (Ashmead), *T. euschisti* (Ashmead), *T. edessae* Fouts, and *T. hullensis* (Harrington); exotic: *T. japonicus* (Ashmead)) and the native parasitoids *Telenomus podisi* Ashmead (Hymenoptera: Scelionidae), *Anastatus reduvii* (Howard) (Hymenoptera: Eupelmidae), and *Ooencyrtus johnsoni* Howard (Hymenoptera: Encyrtidae).

When the rate of emergence of the four most prevalent parasitoid species, *T. brochymenae*, *T. euschisti*, *T. podisi*, and *A. reduvii*, was compared, the mean number of parasitoids that emerged successfully from egg masses attacked by each species varied significantly ( $F = 11.97$ , numerator  $df = 3$ , denominator  $df = 32$ ;  $P < 0.0001$ ). The mean ( $\pm$  SE) number of *A. reduvii* ( $12.92 \pm 2.47$ ) that successfully emerged per egg mass was significantly greater than the other 3 species. *Trissolcus brochymenae* ( $3.38 \pm 0.78$ ) and *T. euschisti* ( $4.0 \pm 1.44$ ) were not significantly different from one another, but were both greater than *T. podisi* ( $0.8 \pm 0.46$ ).

For the four most prevalent parasitoids, the number of egg masses parasitized by each species on each plant genus in native and exotic plots was determined (Table 4). For exotic plant hosts, 14.0% (24/171) of egg masses had developed parasitoids, versus native hosts with 8.9% (15/169); these proportions did not differ significantly ( $P = 0.156$ ). Parasitism by *A. reduvii* did not differ either (4/171 versus 8/169) ( $P = 0.24$ ). However, the proportion parasitized by *Trissolcus* spp. was significantly higher on exotic plant hosts (17/171 for exotic hosts versus 4/169 for native hosts;  $P = 0.0076$ ).

There was a highly significant interaction of plot and plant genus for parasitism rates ( $P = 0.008$ ). There was significantly more parasitism on the native *Prunus virginiana* compared with the exotic *P. padus* and more parasitism on the exotic *Hydrangea paniculata* than on the native *H. arborescens*. Parasitism was also significantly higher on *P. virginiana* than on *Acer*, *Cercis*, and *Hydrangea* in native plots (Fig. 4). The higher rate of parasitism on *P. virginiana* was mostly attributed to *A. reduvii* which parasitized four egg masses compared with only one egg mass each by *T. podisi* and *T. brochymenae* (Table 4). There was also a significant interaction of year and plant genus ( $P = 0.04$ ). Parasitism on *Hydrangea* in 2015 was significantly lower than parasitism on *Acer* in 2015 and



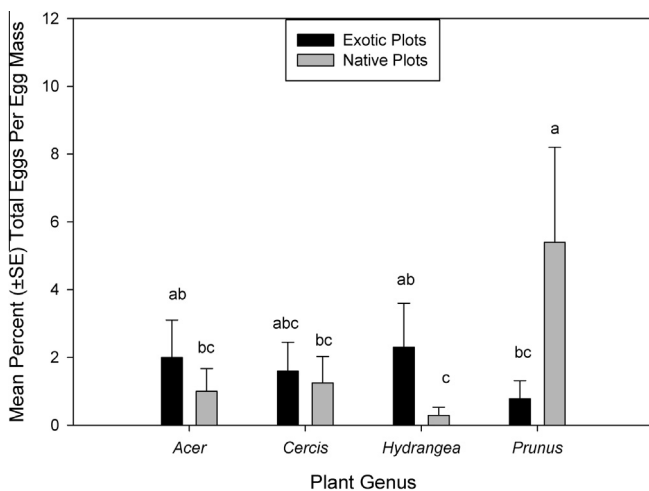
**Table 4**

Number of parasitoids of the four most prevalent parasitoid species collected in each plant genus in exotic and native plots at the National Arboretum from 2014 to 2015. Species were identified from emerged parasitoids and dissected parasitoids.

Plot	Plant Genus	Parasitoid Species	# Egg Masses	Total Number of	
				Emerged Parasitoids <sup>1</sup>	Dissected Parasitoids <sup>2</sup>
Exotic Plots	<i>Acer</i>	<i>Trissolcus brochymenae</i>	3	6	1
	<i>Cercis</i>	<i>Trissolcus brochymenae</i>	2	11	6
	<i>Hydrangea</i>	<i>Trissolcus brochymenae</i>	2	6	0
	<i>Prunus</i>	<i>Trissolcus brochymenae</i>	4	10	0
	<i>Acer</i>	<i>Trissolcus euschisti</i>	1	4	0
	<i>Cercis</i>	<i>Trissolcus euschisti</i>	3	11	3
	<i>Hydrangea</i>	<i>Trissolcus euschisti</i>	0	0	0
	<i>Prunus</i>	<i>Trissolcus euschisti</i>	1	4	0
	<i>Acer</i>	<i>Telenomus podisi</i>	0	0	0
	<i>Cercis</i>	<i>Telenomus podisi</i>	0	0	0
	<i>Hydrangea</i>	<i>Telenomus podisi</i>	2	2	1
	<i>Prunus</i>	<i>Telenomus podisi</i>	0	0	0
	<i>Acer</i>	<i>Anastatus reduvii</i>	2	25	0
	<i>Cercis</i>	<i>Anastatus reduvii</i>	0	0	0
	<i>Hydrangea</i>	<i>Anastatus reduvii</i>	1	23	0
	<i>Prunus</i>	<i>Anastatus reduvii</i>	1	14	0
Native Plots	<i>Acer</i>	<i>Trissolcus brochymenae</i>	1	2	1
	<i>Cercis</i>	<i>Trissolcus brochymenae</i>	0	0	0
	<i>Hydrangea</i>	<i>Trissolcus brochymenae</i>	0	0	0
	<i>Prunus</i>	<i>Trissolcus brochymenae</i>	1	10	0
	<i>Acer</i>	<i>Trissolcus euschisti</i>	0	0	0
	<i>Cercis</i>	<i>Trissolcus euschisti</i>	0	0	0
	<i>Hydrangea</i>	<i>Trissolcus euschisti</i>	0	0	0
	<i>Prunus</i>	<i>Trissolcus euschisti</i>	0	0	0
	<i>Acer</i>	<i>Telenomus podisi</i>	1	1	1
	<i>Cercis</i>	<i>Telenomus podisi</i>	0	0	0
	<i>Hydrangea</i>	<i>Telenomus podisi</i>	1	1	15
	<i>Prunus</i>	<i>Telenomus podisi</i>	1	7	7
	<i>Acer</i>	<i>Anastatus reduvii</i>	1	6	0
	<i>Cercis</i>	<i>Anastatus reduvii</i>	3	26	0
	<i>Hydrangea</i>	<i>Anastatus reduvii</i>	0	0	0
	<i>Prunus</i>	<i>Anastatus reduvii</i>	4	67	0

<sup>1</sup> 17 *Trissolcus japonicus* emerged and one was trapped emerging from an egg mass placed on a native *Acer*. A single *Trissolcus edessae* parasitoid emerged from an egg mass placed on a native *Cercis*. Two *Ooencyrtus johnsoni* emerged from an egg mass placed on an exotic *Hydrangea* and 19 *Ooencyrtus johnsoni*. Emerged from an egg mass placed on a native *Cercis*.

<sup>2</sup> Single *Trissolcus hullensis* individual was dissected from an egg mass placed on an exotic *Hydrangea*.



**Fig. 4.** Mean (±SE) percent of total number of eggs per egg mass parasitized on each plant genus in exotic and native plots over the two-year study; estimated by a generalized linear mixed effects model with negative binomial distribution, log link, and log total eggs offset. Bars with different letters were significantly different (SAS PROC GLIMMIX:  $P < 0.05$ ).

on *Prunus* in 2014. In addition, there was a significant interaction of plot, plant genus, and month for parasitism rates ( $P = 0.04$ ) with parasitism rates reaching their highest level on *Hydrangea* in exotic plots in August and their lowest level on *Hydrangea* in native plots and *Prunus* in exotic plots in July (Table 2).

Females of six parasitoid species were collected attending egg masses. Of the 46 egg masses with attending females, 24 had no evidence of parasitism, 16 were parasitized by the same species as the one collected attending the egg mass, five were parasitized by a different species, one had undeveloped parasitoids, and one egg mass was lost (Table 5). Parasitoids of two species were collected attending the same egg mass five times. Both *T. brochymenae* and *T. podisi* were collected attending the same egg mass twice, and in both cases, only *T. brochymenae* emerged. Both *A. reduvii* and *T. euschisti* were collected attending the same egg mass twice. In one case, *T. euschisti* emerged and in the other, there was no evidence of parasitism. Both *T. brochymenae* and *T. euschisti* were collected attending the same egg mass once, but no parasitoids were found. *Trissolcus brochymenae* was the predominant species collected attending egg masses, comprising 47% of attending parasitoids collected.

### 3.2. Wooded sites

The effect of natural enemies on sentinel egg masses in wooded sites was based on the total number of eggs per mass with nymphal emergence, parasitism or predation. Nymphal emergence, predation, and parasitism rates were evaluated by habitat (wooded sites, landscaped plots) and month (June, July August). Because sentinel egg masses were only placed in wooded sites in 2015, differences between wooded sites and landscaped plots were compared using data collected in landscaped plots in 2015. Overall, there were no differences in the rate of nymphal emergence

**Table 5**

Female parasitoids collected attending egg masses.

Attending Parasitoid Species	Egg Mass with Attending Parasitoid of Each Species <sup>1</sup>			
	No Parasitism	Parasitized by Same Species	Parasitized by Different Species	Unknown <sup>2</sup>
<i>Trissolcus brochymenae</i>	10	11	2	1
<i>Trissolcus euschisti</i>	8	2	0	1
<i>Trissolcus japonicus</i>	0	1	0	0
<i>Telenomus podisi</i>	5	1	2	0
<i>Anastatus reduvii</i>	0	0	1	0
<i>Ooencyrtus johnsoni</i>	1	1	0	0

<sup>1</sup> There were no egg masses with attending parasitoids where parasitoids were identified from dissections.<sup>2</sup> An individual *T. euschisti* was collected on an egg mass that was missing at the time of retrieval.**Table 6**

Number of egg masses parasitized by each species collected from experimental plots and wooded sites at the National Arboretum in 2015. Species were identified from emerged and dissected parasitoids.

Parasitoid Species	# Egg Masses Parasitized in	
	Experimental Plots n = 159	Wooded Sites n = 121
<i>Anastatus reduvii</i>	4	12
<i>Telenomus podisi</i>	2	0
<i>Trissolcus brochymenae</i>	6	1
<i>Trissolcus euschisti</i>	3	8
<i>Trissolcus japonicus</i>	1	0
<i>Trissolcus edessae</i>	0	1
<i>Trissolcus hullensis</i>	1	0
<i>Ooencyrtus johnsoni</i>	2	3

(57.1 ± 3.4%) in wooded sites compared with landscaped plots (52.6 ± 3.1) ( $F = 1.3$ ;  $df = 1, 63$ ;  $P = 0.26$ ). However, the rate of parasitism was more than twice as high in wooded sites (7.7 ± 1.6%) compared with landscaped plots (3.4 ± 0.7%) ( $F = 22.6$ ;  $df = 1, 63$ ;  $P < 0.0001$ ) and the rate of predation was significantly higher in landscaped plots (7.2 ± 1.6%) than in wooded sites (4.3 ± 1.6%) ( $F = 22.6$ ;  $df = 1, 63$ ;  $P < 0.0001$ ). The proportion of eggs in wooded sites with emerged parasitoids was 6.3 ± 1.5% compared with 1.4 ± 0.4% for dissected parasitoids.

The habitat preferences of parasitoid species was evaluated by examining the total number of egg masses parasitized by each species. The six species of parasitoids collected from the wooded sites included *Trissolcus brochymenae*, *T. euschisti*, and *T. edessae*, *Telenomus podisi*, *Ooencyrtus johnsoni* Howard, and *Anastatus reduvii*. In a comparison of the number of egg masses parasitized by each species in the two habitats, wooded sites exhibited higher overall parasitism: 18.2% (22/121), versus 9.4% (15/159) in adjacent experimental plots ( $P = 0.0452$ ). *Anastatus reduvii* was significantly more likely to be found parasitizing egg masses in wooded sites (12/121) versus experimental plots (4/159) ( $P = 0.0143$ ). *Trissolcus* spp. parasitism did not differ between wooded and landscaped sites (9/121 vs. 10/159;  $P = 0.81$ ). Of the four most prevalent species in landscaped plots, two species, *T. euschisti* and *A. reduvii*, were also prevalent in wooded sites. However, no egg masses were parasitized by *T. podisi* and only one by *T. brochymenae* in wooded sites. The three most abundant species in the wooded sites were *A. reduvii*, *O. johnsoni*, and *T. euschisti* (Table 6).

#### 4. Discussion

There were no differences in the rates of parasitism and predation in native plots compared with exotic plots. Overall, the impact of parasitoids and predators was low, accounting for only 8.1% of

egg mortality in landscaped plots and 12.0% in wooded sites. These findings are similar to those reported from a large-scale multi-state, multi-crop study evaluating the effect of natural enemies on BMSB eggs in the eastern US that found overall rates of parasitism and predation of 10.4 ± 2.2% and 7.9 ± 2.2% in 2013 and 2014, respectively (Ogburn et al., 2016).

Although the rate of parasitism was only 3.8 ± 0.8% in the landscaped plots and 7.7 ± 1.6% in the wooded sites, sentinel egg masses are known to underestimate parasitism rates. A study of parasitism on wild and sentinel BMSB egg masses conducted in a woody plant nursery found higher parasitism rates on wild than on sentinel egg masses (Jones et al., 2014). In 2012, wild egg masses had a mean percent parasitism of 28.4% compared to 4.6% in sentinel egg masses, while in 2013 the difference between the two methods increased even further with a mean percent parasitism of 55.3% in wild egg masses compared to 0.8% in sentinel eggs (Jones et al., 2014). A study comparing parasitism rates on wild and sentinel egg masses of the native squash bug *Anasa tristis* (De Geer) (Hemiptera: Coreidae) found parasitism rates of 55.7% on wild egg masses compared with only 21.8% on sentinel egg masses (Cornelius et al., 2016). Moreover, parasitoids can cause egg mortality even when they fail to develop (Cusumano et al., 2012; Abram et al., 2014, 2016). Therefore, parasitism rates on wild BMSB egg masses at the USNA would most likely be higher than those we measured.

Egg predation in the landscaped plots was more than three times higher in 2015 than in 2014. Predation on egg masses in both native and exotic plots was higher in August of 2015 than at any other sampling period in the two year study with the exception of predation in the native plot in July 2015. Egg predation was also significantly higher in landscaped plots than in wooded sites. In August of 2015, several egg masses in landscaped plots were completely removed by predators. In some cases, only the egg shells remained. In a detailed study of predation on BMSB egg masses, Morrison et al. (2016) observed that katydids consumed entire egg masses and that earwigs and ground beetles consumed the contents of eggs, leaving empty egg shells behind. Although predators were capable of having a substantial impact on BMSB survival in isolated occurrences, they did not consistently attack BMSB eggs over the two-year study. Therefore, the overall occurrence of egg predation in this study was low.

There was no overall difference in parasitism rates on different plant genera in the experimental plots. However, there was significantly more parasitism on the native *Prunus virginiana* compared with the exotic *P. padus* and more parasitism on the exotic *Hydrangea paniculata* than on the native *H. arborescens*. Parasitism on *P. virginiana* was also higher than on the three other plant genera in native plots. The higher rate of parasitism on *P. virginiana* can be attributed almost entirely to *A. reduvii* which attacked the most egg masses on *P. virginiana* and had the highest rate of emergence of the four most prevalent native parasitoids. There were also



significant interactions of parasitism rates between plant genera and year and between plot, plant genera, and month, indicating that the impact of native parasitoids on BMSB eggs in cultivated landscapes fluctuates over time and is difficult to predict.

The proportion of eggs that were parasitized was twice as high in the wooded sites as in the landscaped plots. In another study, parasitism rates were higher in a wooded habitat than in an apple orchard and a soybean crop (Herlihy et al., 2016). There were also differences in the species composition of parasitoids in the two habitats. Although *A. redivii* was significantly more likely to parasitize egg masses in the wooded sites than in the landscaped plots, it was the predominant parasitoid emerging from egg masses in both habitats. None of the egg masses from wooded sites were parasitized by *T. podisi* and only a single individual of *T. brochymenae* was found in the wooded habitat. In a study comparing egg parasitism on native stink bugs in woodland and crop habitats in Georgia, Tillman (2016) found that *A. redivii* and *A. mirabilis* (Walsh & Riley) occurred exclusively in the woodland habitat, and that *T. podisi* was the predominant species in both the crops and the woodland. In Maryland, *T. podisi* was the predominant species in soybean crops, but it was not recovered from BMSB egg masses in wooded habitats (Herlihy et al., 2016). Okuda and Yeargan (1988) provided evidence that *T. podisi* and *T. euschisti* partitioned habitats between herbaceous and woody plants. In field experiments, *T. podisi* parasitized significantly more sentinel egg masses of *Podisus maculiventris* (Say) on alfalfa, *Medicago sativa* L., than on hackberry, *Celtis occidentalis* L., and *T. euschisti* parasitized egg masses only on hackberry trees.

There are barriers that restrict the ability of native parasitoids to adapt to exotic hosts, such as an inability to find and recognize them as hosts and/or overcome their physiological defenses (Godfray, 1994). Seven species of native egg parasitoids of Pentatomidae attacked sentinel BMSB egg masses in our study, but they differed in their likelihood of successful emergence. On average, *A. redivii* was significantly more likely to emerge from egg masses, with  $12.9 \pm 2.5$  parasitoids emerging compared with *T. podisi* averaging only  $0.8 \pm 0.46$ . Other studies have determined that *T. podisi* readily oviposited in BMSB eggs, but failed to emerge successfully in the laboratory (Abram et al., 2014; Haye et al., 2015).

In addition, a single egg mass was attacked by the exotic *Trissolcus japonicus*, and a single *T. japonicus* individual was collected attending that same egg mass. High rates of parasitism of BMSB eggs by *Trissolcus* spp. were recorded in China (Yang et al., 2009; KAH, unpublished). Researchers at the USDA ARS Beneficial Insect Introduction Research laboratory were in the process of evaluating *T. japonicus* for potential release as a classical biological control agent when it was first discovered that the species had arrived in North America in Beltsville, MD in 2014 as an accidental introduction (Talamas et al., 2015) and was subsequently discovered in Washington state in 2015 (Milnes et al., 2016). Researchers at the University of California Riverside are also investigating the potential of using *T. japonicus* as a classical biological control agent against BMSB in California (Lara et al., 2016).

*Trissolcus brochymenae* was the predominant species collected attending egg masses and it emerged from 48% of egg masses it attended, whereas parasitoids from the other species emerged from the same egg mass they attended only 22% of the time. Because *T. brochymenae* was frequently collected attending egg masses, it is likely that *T. brochymenae* was guarding egg masses from competitors. Also, *Trissolcus* spp. are known to guard egg masses (Field, 1998; Field et al., 1998; Austin et al., 2005). In contrast, *A. redivii* was prevalent in landscaped plots, but was only collected attending a single egg mass and that egg mass was parasitized by another species, suggesting that *A. redivii* was not actively guarding egg masses.

Cultivated landscapes are predominantly planted with exotic plant species, exacerbating the spread of invasive exotic plants into natural landscapes. Inadvertent and deliberate introductions of exotic plants and arthropods will continually alter trophic interactions in these ecosystems. Exotic species change the structure and composition of native communities in many ways. Therefore, the impact of exotic species in urban landscapes is difficult to predict. BMSB are frequently found on ornamental plants (Rice et al., 2014; Venugopal et al., 2015; Bergmann et al., 2016a,b). Large numbers of adult BMSB overwinter in forested areas and inside human-made structures in urban landscapes (Rice et al., 2014; Wallner et al., 2014). BMSB populations feed on ornamental plants, and adults are capable of migrating among forested areas, urban landscapes, and crops (Venugopal et al., 2015). The complex of natural enemies attacking BMSB will differ in these diverse habitats. In order to develop pest control strategies for managing this invasive exotic species, we will need to evaluate the efficacy of natural enemy complexes in a variety of landscapes.

In the present study, almost 60% of BMSB nymphs were able to hatch successfully from sentinel egg masses placed at the USNA, and only 8% and 12% of eggs were attacked by predators and parasitoids in the experimental plots and the wooded sites, respectively. Although rates of nymphal survival from sentinel egg masses may overestimate survival from naturally laid egg masses, these results suggest that native natural enemies may have little impact on BMSB populations in ornamental landscapes in the Mid-Atlantic USA. If biological control agents are ineffective in suppressing BMSB nymphal emergence in urban ornamental landscapes and surrounding forested areas as suggested by the low parasitism and predation rates observed here, BMSB emigrants from populations in these habitats may hasten the spread of this invasive species into fruit and field crops.

There is conflicting evidence about whether or not native natural enemies are more abundant in native plant communities. For example, native perennials became more attractive to natural enemies as they matured and were more likely to attract more natural enemies than were exotic annuals (Fiedler and Landis, 2007a, 2007b). When we conducted experiments in the same plots used in the current study, spiders were statistically more prevalent in the native plots than in the exotic plots (MHG, unpublished). Alternatively, in cases where exotic plant species increased the abundance of herbivores, natural enemies were more abundant on exotic plants (Lescano and Farji-Brener, 2011; Lau, 2013). In the current study, we tested the impact of natural enemies on an extremely polyphagous exotic pest that feeds and develops on numerous hosts in many genera and families that are represented by related species found in North America and Eurasia. In this case, there were no differences in overall rates of predation and parasitism in native and exotic plots. Moreover, *Trissolcus* spp. were more likely to parasitize egg masses in exotic plots than in native plots. Thus, there is no evidence that native natural enemies attacking eggs of the exotic BMSB were more prevalent in landscapes with native ornamental trees and shrubs than those with exotic trees and shrubs.

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